From exploitation to cooperation: Social tool-use in orang-utan mother-offspring dyads

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Social manipulation represents an important aspect of human social interactions, including cooperative ones. Yet, little is known about social manipulation of conspecifics in nonhuman great apes. We investigated how orang-utan (*Pongo abelii*) mothers used their offspring as a means to access food in competitive and cooperative test situations. In the competitive situations, only the offspring could retrieve high-value food rewards. Here, orang-utan mothers often stole the food from their offspring and even coerced them into retrieving it to begin with, by moving the offspring to the test site, guiding their arms and bodies towards the food, and even re-orienting their hands so that they would grab the food. However, modifying the task constraints so that mothers were now required to cooperate with their offspring to obtain the food changed the mothers' behaviour completely. Suddenly, mothers cooperated with their offspring by handing them tools that only their offspring could use to activate a mechanism delivering food for both of them. We conclude that orang-utans, like humans, are able to flexibly use conspecifics as a social tool and that this kind of social tool-use supports their ability to cooperate.

Keywords:

cooperation, exploitation, great apes, orang-utan, primate cognition, social tool-use

In recent years, the psychological processes underlying cooperation have received considerable research attention from a comparative perspective. Experimental studies have shown that several group-living primate species including chimpanzees, *Pan troglodytes* (Chalmeau, 1994; Crawford, 1937; Hirata & Fuwa, 2007; Melis, Hare, & Tomasello, 2006a, 2006b; Melis & Tomasello, 2013), bonobos, *Pan paniscus* (Hare, Melis, Woods, Hastings, & Wrangham, 2007), capuchin monkeys, *Sapajus apella* (Brosnan, Freeman, & De Waal, 2006; Chalmeau, Visalberghi, & Gallo, 1997; de Waal & Berger, 2000; de Waal & Davis, 2003; Hattori, Kuroshima, & Fujita, 2005; Mendres & de Waal, 2000; Visalberghi, Quarantotti, & Tranchida, 2000), and cottontop tamarins, *Saguinus oedipus* (Cronin, Kurian, & Snowdon, 2005; Cronin & Snowdon, 2008) are able to coordinate their actions flexibly in cooperative problem-solving tasks. For instance, chimpanzees can coordinate with their partners by either carrying out identical (Chalmeau, 1994; Crawford, 1937; Hirata & Fuwa, 2007; Melis et al., 2006a, 2006b) or complementary actions (Melis & Tomasello, 2013) to achieve their objectives.

Temporal coordination is often crucial and chimpanzees can wait until their partners are ready to jointly engage in the task (Hirata & Fuwa, 2007). Furthermore, chimpanzees know who the best cooperators are and actively select them to work together (Melis et al., 2006a). However, given a choice between working with others and working alone, chimpanzees prefer the latter (Bullinger, Burkart, Melis, & Tomasello, 2013; Bullinger, Melis, & Tomasello, 2011; Melis et al., 2006b; Rekers, Haun, & Tomasello, 2011). Also, although some studies found that chimpanzees may help others even if they do not directly benefit (Melis et al., 2011; Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Yamamoto, Humle, & Tanaka, 2009, 2012), other studies did not find such prosocial tendencies (Jensen, Hare, Call, & Tomasello, 2006), and most studies reporting sustained cooperation elicited it in situations in which both individuals would benefit (mutual cooperation). It has therefore been suggested that chimpanzees conceive their cooperators as social tools and that they are - in contrast to humans - not intrinsically motivated to cooperate (Bullinger et al., 2011; Warneken, Gräfenhain, & Tomasello, 2012).

The considerable research effort devoted to investigate the motivational basis of cooperation contrasts with how little is known about how individuals manipulate others as tools. We define social tool-use as the physical and psychological manipulations of animate beings towards some goal. Social tool-use has an instrumental and a motivational dimension. The motivational dimension involves the motives (self- or other-regarding) underlying those manipulations whereas the instrumental dimension involves the actual means-end manipulations of animate beings. We can subdivide the instrumental dimension of social tool-use into four levels depending on the degree of direct physical influence that the tool-user exerts over the social tool. Level 1 represents the highest degree of physical influence since it involves the physical manipulation of others' bodies analogous to the manipulation of inanimate objects. Here, the social tool is treated as an object (not an agent) and the tool-user completely controls it (e.g. pulling the arm of a conspecific to access the food that she is holding in her hand). Level 2 combines the physical control of the social tool with the opportunistic exploitation of self-initiated and -controlled actions by the social tool that are not under direct control of the tool-user (e.g., guiding the arm of the conspecific toward a target object and pulling it back but only after the social tool has grabbed the target object).

Level 3 relies entirely on the social tool's self-initiated and -controlled actions and involves no direct physical control by the tool-user. Here, the tool-user treats the social tool as a self-propelled agent (e.g. passing a tool over to the social-tool who will then act independently of the tool-user but in line with the goals of the latter). This level of tool-use depends on the social tool's willingness to cooperate (either because of their aligned goals or her prosocial tendencies). In the cooperation literature, social tool-use is commonly used in this latter sense (level 3). Finally, level 4 represents the lowest level of direct physical influence on the social tool and involves communication and the psychological effects derived from it (manipulating the social tool by communicating with it without any direct physical interaction; e.g. Bard, 1990). In the current study, we will focus on level 1 and 2 (coercive) and level 3 (cooperative) instances of social tool-use.

Clear-cut cases of social tool-use involve physical manipulations of the tool (i.e., level 1 and 2). For this type of social tool-use to occur (especially when it only results in food for the tool-user), there has to be a power differential between partners. However, power differential is often associated with low social tolerance, which has been identified as a major factor limiting cooperation in chimpanzees (Melis et al., 2006b), macaques (Petit, Desportes, & Thierry, 1992), and capuchin monkeys (Brosnan et al., 2006; Chalmeau, Visalberghi, et al., 1997; de Waal & Davis, 2003). It is therefore not surprising that direct evidence for goal-directed and selective manipulations of others as if they were tools has been rarely documented in cooperative problem-solving tasks. If the power differential between partners is large, social tolerance is low and conversely, if tolerance is high, the power differential may not be large enough to create the conditions for social tool-use to appear. There are some exceptions, however. In an instrumental cooperation task with keas, *Nestor notabilis,* in which one kea needed to operate a lever so that another conspecific could retrieve food from a box, three dominant individuals aggressively approached their subordinate co-operators until the subordinates would push down the lever (Tebbich, Taborsky, & Winkler, 1996). Thus, dominant individuals were enforcing cooperation by means of social manipulations. There is some evidence for social tool-use in primates. In a tool-use task that required throwing stones into a pipe to retrieve a food reward, one Japanese macaque, *Macaca fuscata*, repeatedly used her infants to retrieve the food by actively pushing them into the pipe and pulling them back as soon as they had grabbed the food (Tokida, Tanaka, Takefushi, &

Hagiwara, 1994). When this kind of social tool-use was unsuccessful, the female macaque used a stick or a stone as tool instead, suggesting that she considered her infants as a tool in this problem-solving situation. In another cooperation study, a pair of subadult male orang-utans, *P. pygmaeus,* simultaneously pulled a handle to retrieve food (Chalmeau, Lardeux, Brandibas, & Gallo, 1997). Interestingly, in some instances one of the two individuals pushed the other orang-utan towards one of the handles, thereby, soliciting cooperation – something suggestive of social tool use. Moreover, two adult orang-utans, *P. abelii,* have been found to exchange tokens reciprocally when each individual possessed only tokens that were useless for themselves but that the other individual could exchange for food (Dufour, Pelé, Neumann, Thierry, & Call, 2009). In fact, orang-utans were much more likely to donate tokens to conspecifics, which the recipient could exchange for food with the experimenter, than chimpanzees, gorillas, and bonobos (Pelé, Dufour, Thierry, & Call, 2009).

Thus, orang-utans seem to be a promising species to explore various levels of social tool-use. Mother-offspring dyads in particular might offer the ideal scenario (as suggested by Tokida et al. 1994) because they combine a marked power differential with high levels of tolerance between partners. Mothers' physical strength allows them to steal food resources from their offspring at very low direct costs as they do not have to fear aggressive retribution (which might be the case amongst adults). Moreover, mothers show high levels of tolerance towards their offspring, whose survival (including obtaining food) depend on their mothers for an extended period of time (van Noordwijk & van Schaik, 2005). On the other hand, the balance of power between mother and offspring may be shifted by changing the experimental setup. In particular, creating a situation in which mothers have no direct physical control over their offspring (level 3 social tool-use) may transform the mother's social tool-use from an exploitative to a cooperative activity.

The aim of the current study was to investigate whether and how three Sumatran orang-utan mothers, *P. abelii,* manipulated their dependent offspring as social tools to achieve their goals. We varied the extent to which mothers could physically control their offspring's actions across different experimental situations. We were interested in how flexibly mothers would adjust their manipulations to changing test situations and task constraints. Therefore, we provided the offspring with privileged access to high-value food (competitive situations) or with the exclusive opportunity to activate a mechanism delivering food either to both mother and offspring or only to the offspring (cooperative situation). We examined mothers' response towards their offspring across these situations. In experiment 1, we investigated whether mothers stole high-quality food from their offspring when only the offspring was able to reach it. Crucially, we investigated whether they would manipulate their offspring before the offspring had retrieved the food, to accelerate this process (level 1 and 2 social tool-use). In experiment 2 and 3, we examined whether mothers would also manipulate their offspring to obtain an out-of-reach stick tool that mothers, in turn, could use to retrieve a high-value reward. Finally, in experiment 4, we presented a cooperative situation in which mothers had initial control over the stick tool but this time only infants could use it to operate the apparatus and obtain the food rewards. Thus, mothers could only retrieve the food by giving the tool to their offspring so that the offspring could use it (level 3 social tool-use).

EXPERIMENT 1

Methods

Subjects

Three orang-utan mother-offspring dyads, *P. abelii*, participated in this study. All orang-utans were mother-reared. Two of the juveniles were males. The age of the juveniles ranged between 3 years, 7 months and 4 years. The orang-utans were housed at the Wolfgang Köhler

Research Centre, Leipzig Zoo (Leipzig, Germany). The study complied with the European and World Associations of Zoos and Aquariums (EAZA and WAZA) Ethical Guidelines and was approved by the joint ethical committee of the MPI-EVA and Leipzig Zoo.

Procedure and design

We presented the orang-utan mother-offspring dyads with two different situations, in which juveniles got privileged access to the food. In the first situation, we used a sliding platform that was fixed perpendicularly to a metal frame of a transparent Plexiglas glass panel separating the apes and the experimenter (E). This panel contained three horizontally aligned, circular holes (diameter 6.0 cm) whose small size allowed only juveniles to reach through. We attached a tray on the platform outside of the Plexiglas panel and baited the tray with six grapes (platform situation, see Fig. 1*a*). The tray was out of reach of the mothers but not of the juveniles as the juveniles could pass their arms through the holes in the panel. If necessary, we adjusted the distance between the tray holding the grapes and the Plexiglas panel according to the arm length of the juveniles. After the juveniles had retrieved all six grapes the tray was re-baited for a total of twelve grapes per session. The juveniles retrieved the grapes one by one, i.e. the retrieval of each grape corresponded to one arm insertion. Therefore, each retrieved reward was treated as a separate event. Each mother-offspring dyad received four sessions for a total of 48 events per mother-offspring dyad.

In the second test situation, E placed a food reward (a monkey chow pellet) in the testing compartment adjacent to the one where the mother-offspring dyad was located. The two cages were connected by a sliding door that was closed during baiting. The food pellet was placed 120 cm away from the sliding door so that the mother's arm was not long enough to reach the food when the sliding door was opened. Then the sliding door connecting the two compartments was partly opened (approximately 20-30 cm wide) so that only the juvenile (but not the mother) could slip through (door situation, see Fig. 1*c*). Each dyad received two trials per session and 4 sessions in total. Because for one mother-offspring dyad (Pini and Batak) the juvenile repeatedly resisted his mother's attempts to move him to the room with the food reward (even though Pini moved Batak to the half-opened door in all 4 sessions and tried to push him toward the food in 3 of 4 sessions) we excluded the data of this dyad in the door situation. A human observer was present at all times, to ensure that no harm could be inflicted on the juveniles.

Scoring and analysis

We videotaped all sessions and scored who retrieved the food/tool (first contact with the food/tool), who inserted the tool, who ate the food, and whether the mother manipulated the offspring's actions toward the reward before she could gain access to the food (see Table 1 for the behaviours that we coded as social tool-use). A second coder scored 20 % of all trials to assess inter-observer reliability which was excellent (Cohen's kappa: reward eaten by mother or juvenile: $K = 0.84$, $N = 39$, $P<0.001$; social tool-use: $K = 0.90$, $N = 41$, $P<0.001$).

Results and Discussion

We found that orang-utan mothers ate more than half of the rewards retrieved by their juveniles (Mean ± SE: platform: 64.2 ± 10.2 %; door: 56.3 ± 6.3 %). In every event/trial (100%) in which the mothers ate the reward, the mothers stole the reward from their offspring. Sometimes this involved also removal of food from the juvenile's mouth, who never voluntarily shared the food with their mothers. In 46.0 ± 22.8 % (platform, see Fig. 2*a*) and 91.1 ± 5.9 % (door, see Fig. 2*b*) of events/trials in which the orang-utan mothers got the reward, they manipulated their offspring's actions before their juveniles had obtained the out-of-reach reward. In the platform situation, these social tool-use actions included recruiting the juveniles (i.e. moving the juvenile actively to the platform, mostly by pulling from their arms and legs), pushing their arms toward the food (i.e. pushing the hand of the juvenile through the hole in the Plexiglas panel, sometimes involving squeezing the fingers to facilitate pushing the hand through the hole and turning the arm of the juvenile so that the juvenile's fingers touched the reward, see Fig. 1*b* and Supplementary Movie 1) or pulling the juvenile's arm as soon as she grabbed the food. In the door situation, these actions involved recruiting the juveniles (i.e. bringing the juvenile to the door), pushing them through the half-opened door, holding the juveniles by their arm or leg while the juveniles reached for the food and pulling them back as soon as they grabbed it (see Fig. 1*d* and Supplementary Movie 2). These actions were usually combined in a sequence. In the remaining events/trials in which orang-utan mothers ate the reward (platform: 54.0 ± 22.8 %; door: 10.0 ± 10.0 %), they waited until the juvenile had retrieved it and then stole it.

In 91.1 ± 5.9 % (platform) and 73.3 ± 6.7 % (door) of the events/trials in which we observed social tool-use, the orang-utan mothers ate the reward in the end. In the remaining events/trials, the social tool-use was unsuccessful and the juveniles retrieved the food after their mothers had left the platform or they retrieved and ate the reward in the adjacent cage away from their mothers.

EXPERIMENT 2: SEQUENTIAL SOCIAL TOOL-USE

Having established in experiment 1 that the orang-utan mothers used their offspring as tools to retrieve an out-of-reach reward, we next examined whether they would also use their juveniles to retrieve an out-of-reach tool that, in turn, mothers could use to retrieve food. Thus, the question was whether the orang-utan mothers would be able to sequentially use a social tool to retrieve a physical (stick) tool. We presented the same orang-utan mother-offspring dyads from experiment 1 with situations identical to what they experienced in experiment 1 except that this time juveniles could retrieve a stick instead of grapes.

Methods

Procedure and design

At the beginning of the session, we fixed a tool-use apparatus (see Fig. 3) made of transparent Plexiglas at the mesh of the cage. The apparatus consisted of a horizontal chute (length 25 cm, height x width 4 x 4 cm). At the end of this chute (out of reach of mother and juvenile) there was a hole (diameter 7 cm) in the Plexiglas. Anything that fell into this hole would fall on a ramp and roll toward the mesh. A food reward (e.g. grapes) was placed at the end of the horizontal chute close to the hole. By inserting a stick tool (made of grey PVC, length x height x width 25.0 x 3.5 x 3.5 cm), in this chute, the apes could push the reward into the hole and thus bring the reward via the ramp within reach. The mothers had prior experience with a similar apparatus that required the same type of tool-use.

In the beginning of each trial, E baited the apparatus with a grape (platform situation) / a monkey chow pellet (door situation) in full view of the mother-offspring dyads. The tool was then placed on the platform (platform situation) or in the adjacent room (door situation) out of reach of the mother. The procedure was identical to experiment 1 in every other respect. In the platform situation, the mother-offspring dyads received eight sessions with six trials each; in the door situation, they received four sessions with two trials each.

Results and Discussion

The number of trials in which dyads retrieved the tools varied considerably across dyads, possibly due to the juveniles differing interest in the tool (see Table 2). In particular, Suaq rarely grabbed the tool even when his mother forced him to touch it with his fingers. In every trial (100%) in which the mothers could get access to the tool, they used it right away to obtain and eat the food reward from the apparatus. In all trials in which the juvenile retrieved the tool, the mothers stole the tool from their offspring (i.e. there was no instance of the juvenile giving the tool spontaneously to the mother). In 23.3 ± 19.3 % (platform) and 100% ± 0% (door) of these trials the mothers took action before the juvenile had retrieved the tool in an identical manner to that observed in experiment 1, which included actions like recruiting the juvenile and guiding the juveniles' arm toward the tool (platform situation) or pushing the juvenile through the half-opened door, holding the juvenile by one limb, and pulling the juveniles back as soon as they grabbed the tool (door situation). We observed these actions usually in sequence and in this order. In the remaining trials of the platform situation (75.7 ± 19.3 %), the mothers waited until the juveniles had retrieved the tool on their own and did not physically manipulate their offspring beforehand.

In 81.3 ± 18.8 % (platform) and 87.5 ± 12.5 % (door) of the trials, respectively, in which we observed social tool-use, the orang-utan mothers obtained the tool (and ate the reward). In the remaining trials, the social tool-use was unsuccessful and the juvenile did not retrieve the tool.

These results indicate that in the platform situation, mothers preferred to wait until the juvenile had retrieved the tool and took it away from her only then (except for Padana whose offspring only rarely retrieved the tool voluntarily). In the door situation, mothers lost control over their juvenile if they had not taken action before the juvenile entered the adjacent room. For this reason, social tool-use was more important in the door situation than in the platform situation. This might explain why we observed social tool-use more frequently in the door situation as compared to the platform situation. Together, the results demonstrate that the orang-utan mothers sequentially used their juveniles as tools to retrieve a stick tool, which they in turn used to access the food reward.

EXPERIMENT 3: GOAL-DIRECTEDNESS OF SOCIAL TOOL-USE

Previous experiments established that the orang-utan mothers used their juveniles as tools to retrieve out-of-reach rewards (experiment 1) and tools (experiment 2). Next, we examined the goal-directedness of this behaviour by presenting the same three orang-utan mother-juvenile dyads with a choice between a grape and the tool, a grape and a distractor, or the tool and a distractor. The tool, in turn, could be used to retrieve a higher value reward (a dry food pellet). The distractor had no food-related value. For the juveniles, only the reward had a food-related value, for the mother, the tool had a higher value as they consistently preferred pellets to grapes. We examined whether the mothers directed the juvenile's actions toward the tool contrary to the juveniles' preference to reach directly for the grape.

Methods

Procedure and design

In the beginning of each trial, E baited the tool-use apparatus (see Fig. 3) with a monkey chow pellet in full view of the mother-offspring dyads. Again, we used the two previously established test settings.

In the platform situation, E placed two objects simultaneously on the platform outside the enclosure (i.e. only accessible to the juvenile). E placed the objects in front of the right and left hole of the Plexiglas panel, respectively. In the door situation, one item was placed in the compartment to the left of the mother-juvenile dyad; the other one was placed in the compartment to the right. Subsequently, both doors were opened simultaneously so that the juvenile (but not the mother) could slip through it. The object pairs were either a distractor (a wooden block, length x height x width 6 x 3 x 3 cm) and a grape, the distractor and the tool, or a grape and the tool. The location of each object was counterbalanced across trials. Preference tests confirmed that all three mothers preferred pellets over grapes.

In the platform situation, the mother-offspring dyads received eight sessions with six trials each (each trial type was presented twice per session); in the door situation, there were eight sessions with three trials each (each trial type was presented once per session). An important difference between the two tasks was that in the platform situation the juveniles could retrieve both objects in sequence, whereas in the door situation they could only access one of the items since we closed the other door as soon as the juvenile had left the middle compartment (where the mother was located).

Analysis

We used binomial tests and the Freeman–Halton extension of Fisher's exact test for 2 x 3 contingency tables (Freeman & Halton, 1951). All p-values reported here are exact and two-tailed.

Results and Discussion

Platform situation

When food was on the platform, the juveniles retrieved the food first in most trials (food vs. tool trials: 100%; food vs. distractor trials: 95.8 ± 4.2 %; see Table 3). When the juveniles could choose between the distractor object and the tool, two of three juveniles had a preference for the distractor (79.2 ± 8.3 %). When the juveniles retrieved the food, the mothers ate the reward in most of the trials 63.5 ± 12.7%. In every trial (100%) in which the juveniles retrieved the tool, the mothers took the tool away from the juveniles and used it to obtain and eat the food pellet from the apparatus.

Of the trials in which the mother obtained the food / tool at the end of the trial (mean number of trials ± SE: 40 ± 3), the mothers used their juveniles in 44.0 ± 21.3 % of trials as a social tool. In the remaining trials (66.0 ± 21.3 %), the mothers waited until the juvenile had retrieved the food / tool and took it away from the juvenile thereafter. Following social tool-use, the mothers obtained the food reward in 92.5 ± 2.5% of trials with food on the platform whereas they obtained the tool only in 27.3 ± 5.1% of trials with the tool on the platform. Mothers obtained the tool more often when the other object on the platform was the distractor (46.3 ± 1.9%) as compared to the food reward (8.3 ± 8.3%).

Door situation

When presented with the choice between the distractor and the tool / food, juveniles retrieved the food / tool more often than the distractor (see Table 4). When they retrieved the food, their mothers ate the reward only in one instance (5.6 ± 5.6 %). In contrast, in every trial (100%) in which the juveniles retrieved the tool the mothers took the tool away and used it to obtain the food pellets from the apparatus. The mothers ate the reward that they obtained from the apparatus in every trial (100%).

In every trial (100%) in which the mother ate the reward or obtained the tool, the mother manipulated the juvenile beforehand (Dokana-Tanah: 13 trials; Padana-Suaq: 6 trials). Crucially, we found a significant effect of social tool-use on their juveniles' first decision: juveniles only entered the room with the tool when they were forced by their mothers but went for the food without pressure from their mothers (Fisher's exact test: Dokana-Tanah: $P<0.01$; Padana-Suaq: $P<0.01$). Considering only trials in which mothers tried to manipulate their juveniles (Dokana-Tanah: 14 trials; Padana-Suaq: 9 trials), we found that the mothers obtained the tool in 93.8 ± 6.3% of trials with the tool.

The results of experiment 3 indicate that when forced to decide for one of two options (door situation) the orang-utan mothers influenced the decision of their juvenile by pulling the juvenile toward the room with the tool. When both objects could be retrieved within a given trial (platform situation), for the most part the orang-utan mothers did not influence the first decision of the juvenile (except for Padana whose offspring only rarely retrieved one of the objects voluntarily). Together, these results suggest that the orang-utan mothers' social tool-use was goal-directed and depended on their juveniles' willingness to obtain the food reward or stick tool.

EXPERIMENT 4: SOCIAL TOOL-USE IN A COOPERATIVE SITUATION

In experiment 1-3, orang-utan mothers physically manipulated their offspring like a tool to retrieve out-of-reach food rewards or stick tools. In experiment 4, we investigated whether orang-utan's social-tool use would also extend to situations in which the mothers had no direct physical control over their offspring (level 3 social tool-use). Thus, the question was whether orang-utan mothers would also cooperate with their offspring as circumstances demanded. More specifically, we examined whether orang-utan mothers would pass the stick tool on to their offspring if this was required to retrieve the food.

Methods

Procedure and design

We mounted a slanted tube (length: 340 cm, diameter: 5cm) to the mesh outside the orang-utan enclosure which connected two non-adjacent rooms of the enclosure (room 2 and 4 of the enclosure, see Fig. 1*e*). We baited the tube by inserting uncooked, dried spaghetti fragments (length 10-12cm) into the tube through drilled holes in the tube at two different locations (in front of room 2 and 4). We put a grape and a monkey chow pellet on these spaghetti fragments outside of the tube. When the tool was inserted in the tube in room 4, the tool slid toward room 2 breaking the spaghetti fragments that, in turn, fell down together with the attached grape and pellet. Underneath the tube, we mounted slanted trays (width x depth: 50 x 48 cm) to ensure that the falling rewards would roll toward the mesh of the enclosure. These trays functioned to capture the fallen reward. Due to the inclination of these trays, the reward then rolled towards the mesh of the enclosure. At that point the food reward would become accessible to the apes. We manipulated whether mothers could move to room 4 (where the tool could be inserted, training phase) or whether only the offspring could go there (experiment 4a: test phase) by adjusting the width of the opening between the rooms. In every trial, mothers received the tool in room 2.

As initial training for the mothers, we baited either room 2 or room 4 with a grape and a pellet and opened the doors between room 2 and 4 so that mothers could move between these rooms. After the baiting of the apparatus, mothers received the tool in room 2. All three mothers completed 4-5 sessions for a total of 24 trials (12 trials with room 2 baited and with room 4 baited, respectively).

Like in the previous experiments, Batak did not enter another room without his mother; the data of this mother-offspring dyad was therefore excluded from data analysis. In the test phase, mother-offspring dyads were in room 2 and we baited the apparatus in front of room 2 and 4. We opened all sliding doors (between room 1 and 4) minimally (20 – 30 cm) so that only the juveniles could freely move between rooms. Then mothers received the tool in room 2. We ran 12 trials per dyad.

After Suaq's initial failure to use the tool in the test phase, we presented him with three training sessions in which he was in room 4 and his mother was in room 3. We baited the tube for room 3 and room 4. Suaq received the tool next to the tube in room 4. After Suaq's initial failure we allowed his mother to enter room 4 and to insert the tool (6 trials). Thereafter, Suaq started to insert the tool in the apparatus. We ran another 12 trials to ensure that Suaq would reliably insert the tool in the tube. After this additional training, we presented Suaq and Padana again with the test phase.

Six months after this experiment, we presented the two dyads with a follow-up experiment (experiment 4b) in which again only the juveniles could enter room 4 and we manipulated whether both mother and juveniles were rewarded (as before, room 2 and 4 were baited) or whether only the juveniles would receive a reward when they inserted the tool (room 4 baited only). Again the tool was passed to the mother in room 2. We ran four sessions of six trials each. In session 1 and 3 both rooms were baited; in session 2 and 4 only room 4 was baited.

Scoring and analysis

We scored the same variables as in experiment 1. Additionally, we coded the type of tool-transfer between mother and offspring either as 'active' or 'passive'. We coded an active transfer when mothers held the tool out towards the juvenile and allowed the juvenile to grab it or when mothers slid the tool under the fencing across the floor of room 3 in the direction of the juvenile. We coded a passive transfer when the tool was abandoned by the mother (which happened only twice in the follow-up experiment when only room 4 was baited) or when it was in the mother's possession and the juvenile took it out of her hands, feet, or lap without resistance of the mother and without the mother holding the tool out toward the juvenile. A second coder scored 100% of all trials of experiment 4a to assess inter-observer reliability which was excellent (type of tool transfer: $K = 1.0$, $N = 24$, $P<0.001$; social tool-use: $K = 0.90$, $N = 24$, $P<0.001$).

Results and Discussion

First, we established that mothers were able to operate the apparatus by themselves. All three mothers quickly learnt to solve the task (Padana and Pini in session 1, Dokana in session 2) by inserting the tool on their own and successfully completed 24 trials (12 trials with room 2 baited and room 4 baited, respectively). The juveniles could observe their mothers operating the apparatus during this training phase and in some instances even retrieved some of the food rewards after their mothers had inserted the tool (when room 2 was baited and mothers needed some time to get back from room 4 to room 2).

For the test sessions (experiment 4a), we reduced the opening of the sliding doors so that only the offspring but not their mothers could move between rooms 1 to 4. Then E passed the tool to the mother. In the first trial of the first test session (room 2 and 4 baited), Padana pushed her son Suaq to room 3 and also offered him the tool in room 3. However, Suaq never took the tool to room 4 to insert it into the tube. Dokana did not actively pass the tool on to Tanah in the first trial but she allowed Tanah to take it from her. After having obtained the tool, Tanah went straight to room 4 and inserted the tool which released the food for both mother and daughter. From this first trial onwards, Dokana actively passed the tool on to Tanah by holding the tool out towards Tanah in room 3 or even sliding the tool across the floor of room 3 towards Tanah who was in room 4 (see Supplementary Movie 3).

Because Suaq did not use the tool after his mother had passed the tool on to him, we conducted two additional training sessions with Suaq. After Suaq had learnt to insert the tool reliably (12 trials in two sessions while Padana could watch her son inserting the tool into the tube), we presented Padana and Suaq again with the initial test phase in which the mother received the tool but only the juvenile could insert it in the tube. Suaq and Padana now successfully completed 12 trials and in every trial with Padana actively passing the tool on to Suaq (see Fig. 1*f*, Table 5, and Supplementary Movie 4).

In the test phase, we also observed in total 7 trials with social tool-use including mothers moving their offspring to the door to room 3 and pushing them through the half opened door. In every trial in which the juvenile was within mother's reach when E gave her the tool, she actively moved the juvenile toward the door before passing it on to the juvenile. In two instances, Padana pushed her son through the door and held his leg while she was offering the tool. In one of those instances, Padana only released him after Suaq would take the tool (see Supplementary Movie 5).

In the follow-up experiment (experiment 4b), we manipulated across the test sessions whether only the juveniles were rewarded (room 4 baited) or both mothers and juveniles (room 2 and 4 baited). When room 2 and 4 were baited mothers always transferred the tool actively to their offspring and in some cases mothers manipulated their offspring by moving them towards the door and pushing them through the opening towards room 4 (see Table 6). When only the juveniles could receive a reward, mothers still passed the tool on to the juvenile in the majority of trials. However, the frequency of active and passive tool transfers differed significantly between the two baiting conditions at least for one of the two dyads (Fisher's exact test: Dokana-Tanah: $P<0.05$; Padana-Suaq: $P=0.09$): when only the juvenile was rewarded, mothers were more passive and often would simply allow their offspring to grab the tool after some time. In one trial, Padana did not allow her son to take the tool at all but passed the tool back to the experimenter. Social tool-use was also more frequent for one of the two dyads in the room 2 and 4 baited condition (Fisher's exact test: Dokana - Tanah: $P<0.05$). For the most part (except for three trials), Padana did not even have the opportunity to manipulate her son physically as he stayed in room 3 or 4 (thus beyond his mother's reach) when both got rewarded.

GENERAL DISCUSSION

In the current series of experiments, we systematically documented how orang-utan mothers manipulated their juvenile offspring as a social tool in a flexible and goal-directed manner to obtain a desired object and to activate a mechanism that would eventually deliver food to both of them. In experiments 2 and 3, mothers even used their offspring to retrieve an object that mothers (but not the offspring) preferred. Finally, we showed in experiment 4 that mothers spontaneously cooperated with their offspring by handing them a tool that the latter needed to activate a device that delivered food rewards for both mother and offspring. When only the offspring benefited from the insertion of the tool, mothers' motivation for cooperation declined even though mothers for the most part still continued to hand the tool over to the offspring (or at least allowed them to grab it).

Taken together, these findings show that orang-utans are able to manipulate conspecifics flexibly in order to achieve their goals. This ability can be assumed to support their (and possibly other primates') ability to cooperate. Although chimpanzees prefer to work alone rather than together in problem-solving tasks, they will choose to cooperate when the payoff of cooperative tasks exceeds that of individual tasks (Bullinger et al., 2013; Bullinger et al., 2011; Melis et al., 2006a; Rekers et al., 2011). However, cooperation collapses when the food reward is monopolizable by one individual (de Waal & Davis, 2003; Hare et al., 2007; Melis et al., 2006b) or requires individuals to reciprocate their partners actions over multiple trials (Yamamoto & Tanaka, 2009). Likewise, in the present study we found that orang-utan mothers shifted their strategy from stealing food and tools to donating tools to their offspring to maintain cooperation, presumably based on a self-regarding motivation.

Our results also document the limits of social tool-use and coercion. While the orang-utan mothers manipulated their offspring's actions, they could not coerce them into grabbing the tool (experiment 2 and 3) or inserting the tool into the tube (experiment 4). And in fact, mothers were less successful in retrieving the tool (preferred by mothers but not by the offspring) as compared to the grapes when they manipulated their offspring. The offspring's willingness to cooperate was therefore critical for mothers' success. It is quite likely that the offspring's willingness to cooperate was driven by her own selfish interest in retrieving rewards. However, mothers often passed the tool to their offspring even without obtaining a direct benefit (experiment 4b). This result suggests that orang-utans, at least when there are no costs to themselves, help their offspring in an instrumental task – a finding that has also been reported in chimpanzees (Melis et al., 2011; Warneken et al., 2007; Yamamoto et al., 2009, 2012). However, mothers’ reinforcement history of passing the tool on to their offspring (experiment 4a) might have increased their willingness to cooperate in the current study even when there was no direct benefit for them. It is an open question whether orang-utans would maintain cooperation solely based on other-regarding preferences or by motivating their offspring with some delayed reciprocation (e.g., food sharing). Our results show that orang-utan cooperation is supported by (and possibly grounded in) social manipulative abilities but this does not preclude the existence of prosocial tendencies. The extent to which orang-utans exhibit prosocial motivations to help others is not clear yet and should be further explored by future research.

The cognitive processes underlying physical tool-use might form the basis of social tool use (Byrne & Whiten, 1988). Orang-utan mothers in the current study physically manipulated their offspring in a manner analogous to using a stick (corresponding to level 1 social tool-use). Namely, we detected several important features characterizing physical tool-use in the social realm including sequential tool-use (experiment 2 and 3), goal-directedness (experiment 3), and a dissociation between a tool and its functions (i.e. using a tool for multiple purposes, cf. experiment 1-3 vs. 4). However, the social tool-use observed in the current study went beyond physical tool-use (and level 1 social tool-use) because mothers treated their offspring as self-propelled agents. They expected them to execute certain actions spontaneously (e.g., grabbing the food) that combined with their own manipulations (e.g., guiding their offspring arm) could potentially bring the food within their reach (level 2 social tool-use). More importantly, they expected their offspring to complete a series of actions (without any physical guidance, level 3 social tool-use) that included bringing the tool to the correct location (beyond the mothers' immediate reach) and executing the required action to release the reward.

It is worth noting that Padana started passing the tool on to Suaq already in the very first trial, whereas Dokana started passing the tool on to her daughter after she saw Tanah solving the task once (and continued to do so from the second trial onwards). While Dokana’s performance might be explained by one-trial reinforcement learning, Padana’s spontaneous performance cannot be reduced to reinforcement learning. Thus, social tool-use as documented in the present study might originate from physical tool-use but it cannot merely be reduced to a variant of physical tool-use. Key features that make social tool-use different from its physical counterpart are the actions of the social tool that are not under direct control of the tool user but that are nevertheless taken into account and even anticipated by the tool-user. To what extent orang-utans and other great apes understand causal agency and use this knowledge to manipulate others might be explored by future studies. An interesting question, for example, would be whether orang-utan mothers take their offsprings’ needs and knowledge states into account when they pass on tools. There is already some evidence that chimpanzees take the needs of others into account in a helping task by selectively passing on tools that a conspecific needs to access food (Yamamoto et al., 2012).

In summary, the current series of behavioural experiments showed how orang-utan mothers manipulated their offspring mostly according to selfish motives to obtain high-quality food.

They applied their social tool-use flexibly to achieve their goals. Depending on the constraints of the task they switched from exploitation to cooperation to achieve their goals. This type of social tool-use might form the evolutionary basis for more complex forms of human cooperation possibly forged by the intervention of some forms of other-regarding motives (Tomasello & Vaish, 2013). Future studies should be aimed at investigating whether cooperation can also appear and be maintained in orang-utans based on other-regarding motives or even some form of self-regarding motives satisfied by delayed reciprocation.

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Table 1

Definitions of social tool-use actions.

Type	Level	Description
Pulling	1	Pulling the juvenile’s limb as soon as she grabs the target object to bring it within the tool-user’s reach.
Recruiting	1	Moving the juvenile to the apparatus by dragging, pushing, or carrying her after the reward had been made accessible to the juvenile.
Pushing	1	Pushing the juvenile through the half opened door towards the target object.
Holding	2	Holding the juvenile (located in the adjacent room) by one limb (to prevent her from escaping) until the juvenile grabs the target object.
Guiding	2	Moving the juvenile’s hand and arm through the hole in the panel toward the food reward.
Active transfer	3	Passing the tool on to the juvenile by handing it out or by sliding it over the floor of room 3 towards the juvenile located in room 4.

The level refers to the degree of direct physical control that the tool-user exerted over the social tool (1: full control; 2: partial control; 3: no control).

Table 2

Individual performance in experiment 1 and 2.

	Experiment 1				Experiment 2			
	Platform		Door		Platform		Door	
	ME	ST	ME	ST	ME	ST	ME	ST
Dokana - Tanah	21 / 48	2 / 48	5 / 8	5 / 8	48 / 48	4 / 48	8 / 8	8 / 8
Padana - Suaq	31 / 42	30 / 42	4 / 8	6 / 8	8 / 8	5 / 8	6 / 8	8 / 8
Pini - Batak	36 / 48	15 / 48	-	-	48 / 48	0 / 48	-	-

ME (mother eating): number of rewards eaten by the mothers and the total number of rewards that were retrieved by the juveniles; ST (social tool-use): number of cases of social tool-use. Padana and Suaq received fewer trials but the same number of sessions compared to the other dyads in the platform situation of both experiments because Suaq stopped participating in some sessions.

Table 3

Experiment 3: First choice of the orang-utan juveniles in the platform situation as function of condition.

Trial type	Distractor-Tool		Food-Tool		Food-Distractor	
Dyads (Mother – Juvenile)	Distractor	Tool	Food	Tool	Food	Distractor
Dokana - Tanah	14^{**}	2	16^{***}	0	16^{***}	0
Padana - Suaq	5	3	15^{***}	0	15^{***}	0
Pini - Batak	14^{**}	2	16^{***}	0	14^{**}	2

Binomial tests: **P<0.01; ***P<0.001

Table 4

Experiment 3: First choice of the orang-utan juveniles in the door situation as function of condition.

Trial type	Distractor-Tool		Food-Tool		Food-Distractor	
Dyads (Mother – Juvenile)	Distractor	Tool	Food	Tool	Food	Distractor
Dokana - Tanah	1	7	3	5	6	2
Padana - Suaq	3	5	6	2	6	2

Table 5

Experiment 4a: Performance of the orang-utan mother-offspring dyads in cooperation task.

Dyads (Mother - Juvenile)	Completed Trials	Active / Passive Tool Transfer	Social Tool-Use
Dokana - Tanah	12	11 / 1	3
Padana - Suaq	12	12 / 0	4

Note: Suaq received two additional training sessions with the apparatus.

Table 6

Experiment 4b: Performance of the orang-utan mother-offspring dyads in the cooperation task as a function of the reward distribution.

Dyads (Mother - Juvenile)	**Mother and juvenile rewarded**		**Only juvenile rewarded**	
	Active / Passive / No Tool Transfer	Social Tool-Use	Active / Passive / No Tool Transfer	Social Tool-Use
Dokana - Tanah	12 / 0 / 0	5	7 / 5 /0	0
Padana - Suaq	12 / 0 / 0	1	8 / 3 / 1	0

Figure legends

Figure 1. Illustrations and examples of the experimental set-ups used in this study. *a)* illustration of the Platform situation (experiment 1), *b)* example of an orang-utan mother guiding her juvenile's arm to obtain an out-of-reach reward, *c)* illustration of the Door situation (experiment 1), *d)* example of orang-utan mother holding her juvenile's leg to pull it back as soon as the juvenile grabbed the reward, *e)* illustration of the Tube situation (experiment 4, room 2, 3, and 4 of the enclosure are depicted), and *f)* example of an orang-utan mother giving the tool to her offspring in middle room (room 3) of the Tube situation.

Figure 2. Experiment 1: Percentage of events/trials in which the mother manipulated the juvenile physically in a way reminiscent of tool-use before the juvenile had retrieved the reward. *a)* Platform situation, *b)* Door situation.

Figure 3. Illustration of the tool-use apparatus used in experiment 2 and 3. The orang-utans could access the apparatus from behind the mesh. In this illustration the tool is already inserted in the horizontal chute. By pushing the tool further, the apes could move the reward into the hole and thus bring the reward via the ramp within reach.

700 Figure 1

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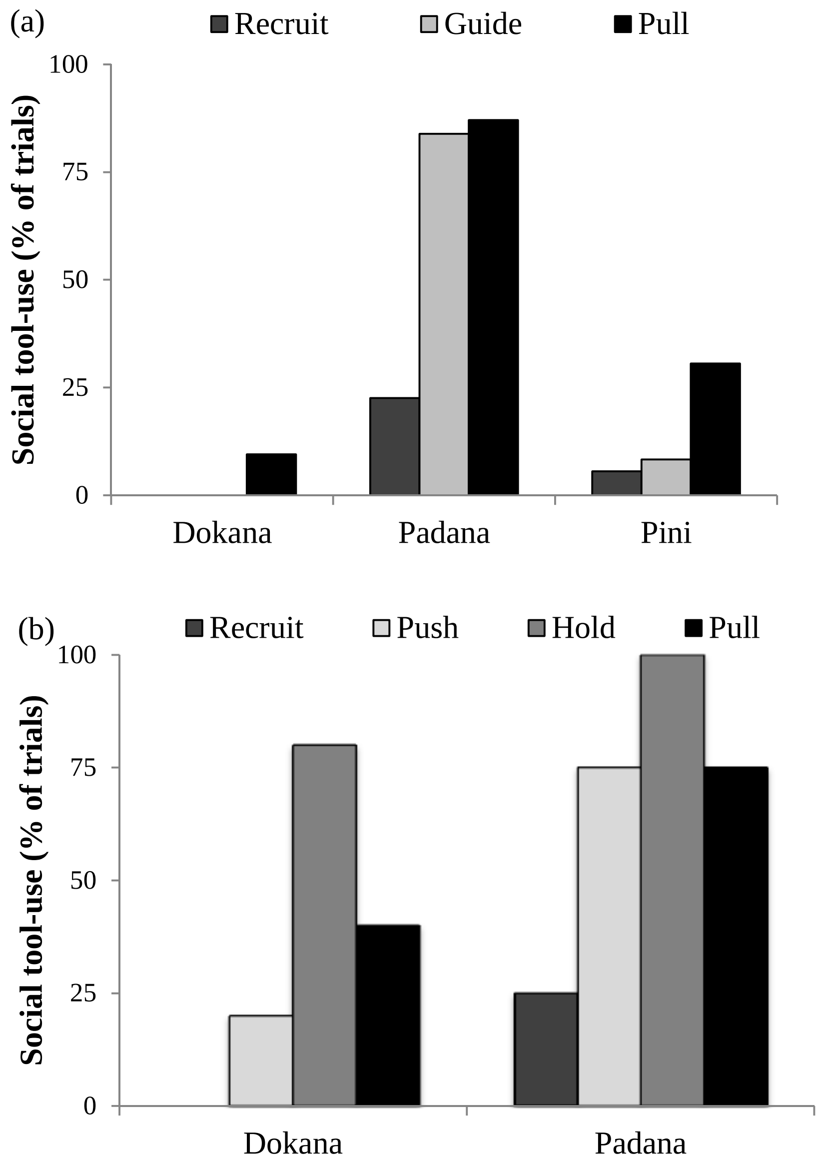
702

Figure 2



(a)
Recruit
Guide
Pull
Social tool-use (% of trials)
100
75
50
25
0
Dokana
Padana
Pini
(b)
Recruit
Push
Hold
Pull
Social tool-use (% of trials)
100
75
50
25
0
Dokana
Padana

Figure 3